

HABITAT (DEPTH) SELECTION IN MARINE ZOOPLANKTON: THEORY AND EXPERIMENTAL TESTS

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LONG-TERM GOALS:

My long-term goal is to achieve a predictive understanding of the vertical distribution and migration of pelagic animals in the sea by assessing the behavioral and demographic responses of zooplankton and micronekton to various combinations of food resources and predation risk.

SCIENTIFIC OBJECTIVES:

First, to test the predictions of a habitat (depth) selection model based on optimization theory by determining the responses of individual zooplankters to various experimentally manipulated conditions of predatory risk and potential feeding rate. Second, to extend the test of the habitat (depth) selection model to field populations of marine zooplankton (e.g., *Calanus finmarchicus* on Georges Bank and *Acartia* spp. in San Francisco Bay).

A related sub-project, entitled "Predation Closure in Modeling the Arabian Sea Pelagic Ecosystem: Model Extension and Data Assimilation", in collaboration with John Steele (WHOI), has two additional objectives: 1) to extend an existing N/P/Z model and apply it to the Arabian Sea; and 2) to compile and assimilate extant field data on zooplanktivores in the Arabian Sea.

APPROACH:

Our overall approach combines experimental, field and modeling techniques. In the case of the manipulation experiments, we took two different approaches. First, we established various combined conditions of mortality risk and potential feeding rate of *Acartia hudsonica* by manipulating enclosed populations of copepods, phytoplankton and zooplanktivorous fish. A subsidiary approach to these manipulation experiments was to investigate the response of *Daphnia* to various combinations of food and predators using the "Plankton Towers" of the Max Planck Institute for Limnology in Ploen, Germany.

The second type of experimental approach employs a newly developed laboratory system which combines video-microscopy with a series of 2-m high columnar tanks, each of which is equipped

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with an infra-red microscopic video cameras on a motorized track that scans the full vertical range of each tank at pre-selected intervals. As described below, this system is being used to test variations of the habitat (depth) selection model, e.g., the role of predator-mediated chemical exudates in triggering migration behavior in zooplankton and the role of vertically heterogeneous food resources (or "thin layers") in modulating the vertical distribution and DVM of zooplankton.

In the case of the comparative field study, we are using observations on the vertical distribution and DVM behavior of copepods from two on-going field programs with which I am associated. The first data set will be *Calanus finmarchicus* on Georges Bank collected during 1994-96 under the aegis of the US Global Ocean Ecosystem Dynamics (GLOBEC) Northwest Atlantic/Georges Bank Field Program. The second data set will be for *Acartia* spp. collected during 1996-98 in collaboration with the US Geological Survey's Water Quality Monitoring Program of San Francisco Bay.

For the modeling studies, the focus is on using an existing N/P/Z model (Henderson and Steele, 1995) with vertical structure and applying it to the Arabian Sea, to demonstrate the different patterns in P(z) resulting from vertical migration (a) to escape predators and (b) to search for food. A specific development related to the Arabian Sea uses a 2-layer (x-z) N/P/Z model to study the consequences of variable vertical migration in upwelling filaments. To help "close" the model, empirical data on predator distribution, abundance and diet will be compiled from (a) the literature (of particular interest and priority for us is to access the rich data sets possessed by Ukrainian scientists) and (b) collections made in 1995 from the RV MALCOLM BALDRIDGE using a Multiple Opening-Closing Net/ Environmental Sensing System trawl (MOCNESS) between ca. 1000 m and the surface.

WORK COMPLETED:

Several important tasks have been completed to date, including: 1) field manipulation experiments assessing the response of *Acartia* to various concentrations and distributions of food (phytoplankton) and zooplanktivorous fish (*Gasterosteus aculeatus*, the threespine stickleback); 2) experimental tests of the depth selection model as applied to *Daphnia* using the "Plankton Towers" of the Max Planck Institute for Limnology in Ploen, Germany; 3) participation in the multi-ship, multi-investigator GLOBEC Georges Bank Field Program (one cruise as chief scientist and four separate cruises for my laboratory group in 1995; two other cruises in 1997); 4) extension and application of an NPZ model to simulate the coastal upwelling of the Arabian Sea; 5) compilation of extant data on the distribution, abundance and diet of zooplanktivores in the Arabian Sea; and 6) processing of macrozooplankton and micronekton samples from the 1995 Baldridge cruises in the Arabian Sea; and 7) participation in monthly USGS cruises in San Francisco Bay between December, 1996 and October, 1997; and 8) development of a new experimental system in the laboratory which combines video-microscopy with a series of 2-m high columnar tanks.

RESULTS:

Our results to date include experimental, field and modeling results. The first set of manipulation experiments used 2.3 m³ field enclosures (mesocosms) to examine the response of *Acartia* to various concentrations and distributions of food and zooplanktivorous fish. These conditions led

to very specific model predictions as to "trade-offs" between foraging and predator avoidance, and by extension, predictions of the vertical distribution and diel migration patterns of the copepods. Comparison of the predicted versus the observed copepod distributions over several days and nights resulted in a statistically significant correlation, indicating that the model has good predictive capability as to where and when the copepods will be distributed vertically.

The second experimental test of the habitat (depth) selection model used *Daphnia* in the "Plankton Towers" of the Max Planck Institute for Limnology in Ploen, Germany. Here too both food (algae) and predators (sticklebacks) were manipulated in various combinations during the course of several experiments. In total the model was able to predict 29 of 31 vertical distributions of *Daphnia* subjected to a wide range of experimental conditions.

Our newly developed experimental system combining video-microscopy with a series of 2-m high columnar tanks has proven itself an invaluable tool for our studies of zooplankton vertical distribution and diel migrations. Each tank is equipped with infra-red microscopic video cameras on motorized systems that scan the full vertical range of each tank at pre-selected intervals. Each tank has a series of valves to allow for adding or withdrawing water samples for manipulation and/or analysis of nutrients, chlorophyll, etc. A dawn/dusk light simulator adjusts the light over each 24-hr period. Zooplankters ≥ 0.25 mm are seen as shadows and recorded on a VCR. Using *Acartia* spp. as test organisms, we are focusing our current experiments on two main areas: first, the role of predator-mediated chemical exudates in triggering migration behavior in zooplankton; and second, the role of vertically heterogeneous food resources (or "thin layers") in modulating the vertical distribution and DVM of zooplankton.

Results of the N/P/Z modeling in the Arabian Sea are as follows: the upper layer moves off-shore at 10 km/day (or 10 cm/sec); the lower layer is stationary. The upwelled water has 10 mm/m³ nitrate and negligible P and Z. The initial conditions are low N,P,Z. The model was then run with the zooplankton spending 18 hrs/day feeding in the moving upper layer and 6 hrs stationary in the lower layer. After 20 days there is near equilibrium, where the pattern going off-shore mimics the traditional N,P,Z development with time. If, however, the time in the upper layer is only 6 hrs/day but the overall grazing pressure is the same (i.e., the rate is x3) then very different patterns develop in N and P. In particular the levels of P (i.e., chlorophyll) are about one-third the previous case and significant nitrate concentrations extend three times as far off-shore.

Results to date from the Arabian Sea empirical studies indicate that the midwater fishes *Cauliodus* spp. and *Stomias* spp. are important predators on myctophid fishes (whose vertical distribution and diel migration behavior they "track" closely), but not of herbivorous zooplankton.

IMPACT:

We have extended optimization theory used previously in other fields of ecology to the study of pelagic ecology to test a priori hypotheses about where, when and why zooplankton position themselves in the water column. Our results to date with the marine copepod *Acartia hudsonica* and the freshwater cladoceran *Daphnia hyalina* suggest that these animals are responding to the presence of both predators and food, and most importantly, are able to assess both simultaneously and make trade-offs between the risks of predation and the gains of foraging and

in their choice of habitats (depths) in which to reside. This research is relevant to the Navy interests because zooplankton and micronekton dominate the scattering of sound in the water column at frequencies between 10 kHz and 10 MHz; the Navy must therefore be able to predict where and when sound scattering layers will occur. Moreover, this research is broadly relevant to oceanic biology, for depth selection is important not only in population biology and community ecology of zooplankton, but also in understanding the vertical flux of materials, nutrients and energy from surface waters to depth in the ocean.